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Effect of Varied Disturbance Types on Dorylus (Anomma) molestus Defensive Behavior in the West Usumbara Mountains, Tanzania.

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ABSTRACT

The purpose of this study was to observe novel nest characteristics of *Dorylus molestus* (Siafu), as well as their defensive behavior in response to varied disturbance methods. The number of defensive soldiers at a specific section of a column was counted before and after each agitation. Varied agitation methods were used on columns without larvae presence to test how soldiers responded to different disturbance types. Disturbances on columns with larvae presence were compared to those on columns without larvae. Nest distribution, behavior, composition, and size were observed objectively. Mechanical disturbance was found to incite the greatest increase in defensive soldier presence. Columns with larvae presence had a greater increase in soldier presence than columns without larvae present. Nests were largest in areas with the greatest protection and cover, and were found most commonly in areas of fragmentation. The ants possess complicated modes of communication through chemical reception, and are able to relay specific reactions to each other in response to varied types of agitation. Also, this species possesses a key role in the balance of the ecosystem, specifically with prey populations. The importance of Siafu behaviors in conjunction with the rapidly changing ecology of the region could have serious implications for agricultural practices and prey population dynamics.

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INTRODUCTION

Polymorphism, or the morphological difference in workers, occurs in roughly 20% of ant genera. The implications of these morphological differences suggest that division of labor within ant subgroups has selected for drastically larger ant classes, finely tuned for colony defense, raid support, and other specialized functions. The specialization of caste roles within a colony represents relative behavior inflexibility on an individual basis, meaning that the roles of individual ants are limited because of their morphology. The stark polymorphism of ant families, such as the African Driver Ants (*Dorylinae*) of Tanzania, represents an evolutionary strategy that appears most suited to tropical climates, where the environment and climate, and inherent selective forces, are fairly consistent year-round (Oster & Wilson 1978). Detailed information about this species of ant in Tanzania is almost non-existent, and many of the observations made in this study could be unclassified in scientific literature.

Revered for their aggression and fierce predatory behavior, driver ants (Siafu) represent one of the 44 genera displaying dynamic polymorphism. Siafu are widespread in Central and East Africa (Garey 2015), and can be found in diverse ecosystems, from the savannahs of the Serengeti all the way up to sub-montane tropical forests of the Usumbara Mountains. A single colony can boast up to 22 million individuals, enabling them to wipe areas clean of insects and small animals (Raignier & van Boven 1955). However, the success of these predators is not entirely contingent on their numbers alone. What sets the Siafu apart from the endless amount of other insect predators in the region is the efficiency of their caste systems, and the ability to conduct tasks concurrently rather than sequentially (Oster & Wilson 1978). The ability for these insects to manipulate their environments so effectively has granted them the title of a keystone species, meaning that the impact that they have on their ecosystem is disproportional to their biomass. Areas raided by ants have been found to greatly reduce arthropod diversity, creating patches of populations in different stages of recovery (Berghoff et al. 2003). This prevents the emergence of climax communities in local environments, a phenomenon that could be explained by the intermediate disturbance hypothesis

The response of a colony to specific stimuli is supplemented by the caste system, in that different individuals are suited for different tasks, allowing for a large-scale response that is both efficient and prompt. Also, the failure of one individual at a specific task is secured by the fact that one of the other million or so individuals in that specific caste are likely to succeed. The "super organism" of the Siafu, in this way, has a great advantage over any individual predator in that it is less dependent on all of its parts performing perfectly (Oster & Wilson 1978).

In the Siafu colony, there are four distinct castes: the queen is the largest of the subtypes, followed closely by the winged drones, or males. These males are commonly called "Sausage Flies" for their elongated body shape, and exist solely for the purpose of mating with the queens of other colonies (Schabel 2006). The soldiers represent the defense of the colony, with enough force in their mandibles to break skin, and even hold wounds together like sutures on a cut (Garey 2015). The workers are the smallest caste, and perform a variety of tasks such as tending to the queen, building walls, foraging for food, and defending the colony. A study by Braendle et al. (2003) found that Dorylus workers of larger sizes were more likely to participate in colony defense. It is believed that this soldier class of ants in more actively found in nests in order to guard the queen, the individual that holds the colony together. The death of the queen signals the collapse of the colony, meaning that the remaining workers and soldiers must disperse and join another colony or die (Garey 2015; Oster & Wilson 1978).

While many studies have explored ant physiology and taxonomy, only a few have focused on ant communication and defensive habits for aggressive subspecies such as the Siafu. Ants are known to communicate mostly by pheromones, touch, and sound. Successful ants foraging for food leave a trail of pheromones on the ground, which grows stronger and stronger as more ants build up along it. This negates the need for a specific ant to remember where a food item is, or a possible attacker, because the pheromones that it releases serve as a marker for itself and for other individuals (Jackson & Ratnieks 2006). In army ants, studies have shown that multiple pheromones are used in order to coordinate fast raids of areas in search of food. How these chemical signals are used in coordinating defense of nests and columns is not completely understood. More importantly, how these signals are affected by human disturbances, such as brush fires or traffic, has not been studied.

With increased degradation of the environment in habitats such as the Usumbaras, species like the Siafu will come into greater contact with humans. How this contact will effect the populations of Siafu in the area is important in predicting environmental shifts in terms of population dynamics of insects and other prey species. Increased trash burning and fragmentation of the forest due to the increase in shamba area in the mountains is concerning given the degree of endemic species in the tropical forests. Garey found that Siafu were affected by different modes of disturbance, including the rerouting of columns in exposure to increased sunlight (2015). How this species of ant will react and persist in the face of increased amounts of burning, fragmentation, erosion, and human traffic remains relatively unexplored. How the ants distribute their defensive resources in response to human-caused stimuli could have important implications into how they will survive with increasing human presence. If the ants allocate increased defense in one area, inherently they would have less resources to move in case of disturbance somewhere else in a column. In this way, human presence could seriously affect the composition and health of ant colonies in the region.

In this study, the effects of different disturbance methods were tested on columns to see whether soldier presence was heavier for a specific type of disturbance compared to another. Mechanical disturbance, water disturbance, and fire disturbance were used to disrupt columns and incite a defensive response from the ants. The reactions of the column to each of these disturbance types were observed and recorded. This study also objectively explored novel column and nest behavior, composition, distribution, and structure. I hypothesize that 1) soldier presence will increase the most in columns that have eggs and larvae, 2) soldier presence will increase the most after a fire disturbance, and the least after a water disturbance, and 3) column flow will be delayed the most after more aggressive forms of disturbance.

MATERIALS & METHODS

Site Description – (Map Located in Appendix A)

Data collection was performed in the West Usumbara Mountains of Tanzania. The Usumbara Mountains comprise part of the Eastern Arc Mountain Chain, and are home to numerous endemic species (Heinen 2006). This island effect of biodiversity is in part created by the surrounding savannah ecosystem, which acts as a barrier for the movement of species into and out of the montane-rainforest region (Garey 2015). The value of these mountain forests as a habitat for undiscovered flora and fauna makes them an important resource for future research. The Mazumbai Forest Reserve (MFR), maintained by Sokoine University of Agriculture (SUA), houses an unknown number of these endemic species. A virtually untouched tropical forest, the reserve lies at 4°50' S, and 38°30 S, with a slope of 1300masl (meters above sea level) East and 1900masl West (Hansen 2007). The 320 Ha of forest is guarded year round by employees of the MFR, and contains only a few man-made trails and footbridges.

The area boasts an impressive amount of rainfall, averaging 1,230 mm and roughly 125 days of rain per year (Redhead 1981; Iverson 1991). As a result, tropical trees and vegetation are abundant in the area. Over the past 40 years, however, increasing habitat fragmentation has occurred, partially due to the enormous population growth of the local peoples. In the 1970's, an increase in the amount of tea grown in the area supplemented the deforestation (Karl 2006). Illegal cutting for firewood and rare wood species continues to plague the region, meaning the tropical forests are in a perpetual state of emergency.

The surrounding land outside of the reserve is primarily farmland (shamba) for the local Wasambaa people. The shambas East and North of the MFR, part of the Sagara Village, are composed of fragmented bits of forest that have been partially clear-cut by the people in order to grow cash crops such as tea, bananas, sugarcane, and maize. The stratification of crops in the local communities creates a conglomerate of microenvironments ranging from open shrub land and dirt plots to forested groves and riverbeds. The shambas are bisected by numerous footpaths and a public-access road that runs north to south (Hansen 2007). Footpaths were detrimental in traversing the shambas in search of ant columns, and allowed for faster movement and longer observation time.

Ant column observations were taken both within the MFR and in the nearby shambas of Sagara. Given the scarcity of paths inside the forest, as well as the heavy vegetation, more observations were taken in the shamba areas and edge lands than in the rainforest itself. The most successful method of finding columns was by scouring the roads and footpaths for places where the ants crossed. The columns were easily recognizable as dark, raised bands thick with mobile ants.

Column and Nest Discovery

Columns were found primarily through hiking and searching along paths in the shambas and villages. Villagers were also asked if they had seen any ant activity in the area, and were very helpful and eager to assist. Nests were found by following columns in either direction of ant flow. A large nest was situated close to the Chalet where I was staying, which made discovery and experimenting much simpler. 33 columns and 7 nests were used for observations.

Ant Identification and Behavior

Ant subgroups were identified by size and shape. Soldiers were characterized by their enormous head size and mandibles. Guarding soldiers were recognized as being immobile, with mandibles extended for at least 15 seconds. Ants outside the frame of the camera were not counted. Ants partially inside the frame of the camera were counted. Other ant subgroups were not included in this study.

Selection and Filming of Columns

Data collection was taken between 8:00 a.m. and 12:00 p.m., and 4:00 p.m. and 6:00 p.m. Ant columns were chosen non-randomly by ease of access. Footpaths and roads were used to navigate the terrain. When a column was seen on or near the paths, we would follow the column away from the path at least 5 meters in order to negate the effect of human traffic disturbance. Sections of the column were chosen randomly either on the same column or on separate columns. Separate columns were characterized as being at least 30 meters away from each other. Disturbed sections of the same column were performed at least 10 meters apart. Column sections were only selected if they had high to medium ant density, meaning that the distance between marching ants was one body length or less.

Two types of ant columns were selected for disturbance: those with larvae present (LP), and those with larvae absent (LA). LP columns were characterized as those that had visible larvae being transported in a constant stream. LA columns were those that had no visible larvae being carried by workers for a time period of at least 3 minutes. All filming was done on an iPhone 5 C using a makeshift stand from the whorls of a tree branch. The stand was stuck into the ground so that the camera was approximately five inches off the ground and looking down directly over the column. Filming was not performed in heavy rain due to the limitations of the camera and the bias of the water disturbance. After a rain, filming did not resume until 1 hour of no rain had passed.

Disturbance of Ant Columns

A total of 120 sections of columns were disturbed. 30 were performed for each experiment: mechanical (for both LP and LA), fire, and water. The experiments were performed on 3 LP and 33 LA columns. Column sections were filmed for 1 minute before the disturbance, and 5 minutes after. The number of soldiers guarding before the disturbance and after were counted. Three disturbance methods were used on the ant columns: mechanical disturbance, water disturbance, and fire disturbance. Disturbances on LP columns were limited to mechanical disturbance due to the sensitivity of the larvae and the importance of them to the colony's survival.

- Mechanical disturbance was performed with a human finger, or a stick of equal circumference, swiftly dragged perpendicular to the flow of the column three times.
- Water disturbance was performed with an O2 Cool Mist 'n Sip water bottle, squirted directly over the ant column once.

- Fire disturbance was performed with a 3 x 5 in. piece of paper, folded once lengthwise. The paper was lit on one end with a Bic lighter, and placed directly on the path of the ants. After it was extinguished, or after 10 seconds of burning, the paper was carefully removed with a stick. Fire disturbances were not performed inside the MFR due to fire hazard.

Time Observations

The amount of time that it took for the column to resume normal ant flow was recorded for each method of disturbance. 90 times were recorded in total only for the LA columns, 30 for each of the 3 disturbance types. Normal flow was measured observationally before the disturbance and after on the basis of ant density. When the column density after disturbance matched that of it before, it was considered normal flow. If the column did not return to normal flow, the behavior was noted and time was not recorded. Time observations were note recorded for egg columns due to the infrequency of their occurrence.

Nest Observations

7 nests were found in the duration of this study. Observational data on nests were recorded on the basis of access. Whenever a nest was found, video recordings or photos were taken. Nest area was estimated in square meters. Nest cover by trees and by vegetation was estimated separately as percentages. Materials composing the nest were recorded, as well as the environment where the nest was located. Any notable behaviors and trends were also recorded. Nests were often difficult to observe due to heavy vegetation and aggressive ant behavior near the nest. Descriptive statistics were used to describe the nest characteristics.

Statistical Tests

An unpaired T-Test was used to compare the mean soldier increase in LA and LP columns after mechanical disturbance. A one-way ANOVA was performed to test the difference in mean soldier increase after disturbance in LA columns, agitated with mechanical, fire, and water disturbances. A Tukey's post-hoc test was used to discern differences between each type of disturbance. A one-way ANOVA with a Tukey's post-hoc test was performed to test if the mean amount of time it took for columns to return to normal flow was different for each of the three disturbance types on LA columns.

Biases and Limitations

- It was difficult to film in the rainy season because my phone was not waterproof. It rained on most days and forced me to take more videos in a shorter period of time.
- The columns I chose were selected because of how easy they were to access. This meant that they were either close to roads, near houses, or land that was relatively exposed or close to humans.
- I accidentally disturbed some sections of the columns by stepping on them, which could have affected the sections I sampled nearby.
- Ants would get upset if they caught the smell of my breath, or if I breathed on them by accident.
- Ant activity was not measured during the middle of the day because of the heat's effect on the ants' activity.
- Some of the workers look very similar to soldiers on the film, and the perspective of the camera made it difficult to identify soldiers at some points.
- Nests were hard to find because it was often impossible to keep following a column through thick vegetation and rough terrain.
- The fire tests would sometimes get too close to my phone's camera
- The ants are nomadic, and often times the places that I found them were not suitable to perform tests.
- My phone could only hold 8 videos at a time, which inhibited my ability to collect data for extended periods.
- Francis, my guard, would often use his machete more often than he needed, and would disturb sections of the columns or the nests.

RESULTS

Ant columns and nests were observed between April 5th and April 19th, 2016 in and around the Mazumbai Forest Reserve in the West Usumbara Mountains. The focus of this study was to observe *Dorylus molestus* (Siafu) soldier presence and defense responses, as well as column flow rates, due to different disturbance methods in two column types. This study also sought to better understand Siafu nest structure, distribution, behavior, and composition. Photos and videos from this study can be accessed online (Appendix B).

Observational Results

Ant columns and nests were observed for notable behavior, composition, and distribution. Specific attention was given to aspects of Siafu behavior explored and highlighted by Garey (2015). These observations are taken on the basis of estimations and trends seen by the observer, and are not prepared for statistical analysis. It is the hope of this study that these observations will aid in future scientific studies on Siafu behavior.

1. Behavioral Observations of Columns and Nests

1.1 Scaffolding

Siafu columns were observed demonstrating scaffolding behavior, particularly in higher density areas of ants, and in areas of continual disturbance such as roads. This behavior is the linking of ants in a Velcro-like mesh, usually covering the top or lining the sides of a column. The meshwork of ants stays connected even when being prodded by a stick, and only disperses in the presence of fire or water. Ant scaffolding was most commonly found in areas where the ground was very firm or unfavorable, such as on roads, rocks, cement, and near puddles. Scaffolding was most commonly seen in LP columns.

Scaffolding in ant nests was observed for two days only in the Mazumbai Forest nest. The ants were seen creating a sheet of bodies, roughly 20 cm tall and 10 cm wide spanning the opening of the nest. The wall dissipated quickly after disturbance.

1.2 Workers and Soldier Composition Without Disturbance

I found at least 6 different morphs of workers by sampling columns, ranging from 2 mm to 12 mm (Fig.1). 2 different sizes of soldier-like morphs were observed; differing by about 1 mm. Legions of soldiers were most commonly found in the openings of tunnels and under leaves that overlapped with columns. These garrisons tended to appear more often around midday, especially when it was sunny and warmer, with little or no rain the night before. Other soldiers were seen providing a variety of tasks for the workers within columns. This behavior will be described in more detail in the discussion.

More soldiers were seen in and around nests than guarding columns. Soldiers would remain stationary at the mouths of nests, or moving slowly inside of them. Soldiers made up a majority of the ants in nest scaffolds, whereas workers did in column scaffolds.

1.3 Reactions to Other Insects

Areas close to a raid or nest site were found to be largely bereft of other insect life. LP columns were found to ignore food items and insects more often than LA columns. Areas close to foraging ant columns could be identified by the lower abundance of jumping crickets and grasshoppers.

Ants occupying a nest were not as likely to attack small insects that were inside the nests. Small arthropods and silverfish could sometimes be seen moving around the ant masses inside the nest.

1.4 Repeat Disturbances

Ant columns on roads tended to have a greater number of ants in scaffolding formation, as well as guarding soldiers around the column. Columns on roads could easily be seen from a far distance as a result of their increased width and height off the ground. Scouting ants could also be seen moving perpendicular to the column movement, roughly 10 meters in either direction in the middle of the road. These ants would aggressively attack anything they encountered.

2. Distributional Trends

2.1 Exposure, Distribution, and Nest Shape

Columns tended to stay under cover whenever possible (Table 1). In areas where cover was scarce, columns navigated to remain as shaded as possible. In places where the column was exposed to sunlight, ant scaffolding occurred over the top of the column.

Nests tended to be found on banks or slopes of hills. Nests were often shaded by either treetop cover or vegetation (n=7). Nests with more cover tended to display slightly larger diameters than those in more open terrain. The nest found in the forest was much larger in diameter than any of the other nests found in the shambas or in the grass. Most nests were found in tilled shamba fields below the MFR. Nests were most often composed of excavated dirt.

3. Other Nest Characteristics

3.1 *Structure*

Nests do not seem to be a labyrinth of tunnels like other ant species. Nests are normally large hole in the ground that is supplemented by other tunnels. Nest sites seem to be chosen on account of how easily accessible they are. Grassy embankments with overhangs, dirt caverns at the roots of trees, and piles of leaf litter seem to attract ant nests. Most often, nests took he shape of whatever terrain they were embedded in, which excavated dirt and debris surrounding.

3.2 *Movement*

The movement of one nest and subsequent building of another was observed near the Chalet. The original nest was found on April 8 at 9:00 a.m. north of the Chalet with a LP column flowing away from the site. By following the LP column, another nest site was discovered roughly 200 meters from the original towards the south. The nest was approximately 20 meters away from a large garbage pile filled with rotting food and insects. Columns exuding from the nest moved towards this pile, presumably to gather food, for 4 to 5 days. Raids were found periodically in various patches of land around the nest. The areas of the raids would change, sometimes twice daily. This nest remained here until April 14 when it was found abandoned, with LP columns extending from it heading south.

Experimental Results

Disturbances of LP and LA columns were measured for changes in guarding soldiers before and after the agitation. All disturbances revealed a higher mean soldier presence after each disturbance than before on average. The amount of time that it took for the ant column to resume normal flow was also measured. The selection of columns was non-random, with multiple notations being taken on one column.

4. Larvae Present and Larvae Absent Disturbances

4.1 Soldier Presence After Mechanical Disturbance (LP and LA Comparison)

The number of guarding soldiers after mechanical disturbance was found to be greater on average in LP columns than in LA columns ($p<0.0001$) (Fig. 1).

4.2 Varied Disturbance Types on LA Columns

The greatest average number of soldiers was found after mechanical disturbances on LA columns ($p<0.0001$)(Fig. 2). Fire disturbances displayed the second highest increase in soldier presence, followed closely by water disturbances.

4.3 Delay of Column Flow After Disturbance

The time that it took columns to resume normal flow was found to differ between disturbance types (Fig. 3). Fire disturbance caused the longest delay of column flow, with two columns failing to resume flow at all. Mechanical disturbance delayed the columns slightly more than water disturbance.

4.4 Action of Columns in Response to Disturbance

All of the columns disturbed by mechanical agitation and water eventually continued on the same route. Most of the columns rerouted around the area of the burning after a fire disturbance (Fig. 4). Several of the columns continued through the area of the burn, and a few turned around completely and abandoned the column track.

Figure 1. The 6 different subtypes of workers in the Siafu colony.
The individual on the far left is a soldier.

Table 1. Locations, sizes, percent cover, and composition for Siafu nests within and around the Mazumbai Forest Reserve (n=6). Values are taken as estimates.

Nest Location	Nest Size (m^2)	Nest Cover by Trees (%)	Nest Cover by Vegetation (%)	Nest Material
Shamba	1.5	15	100	Dirt Pile
Shamba	2	0	100	Dirt and Grass
Grass Field	1	0	25	Dirt Pile
Grass Field	1	10	50	Dirt Pile
Forest	5	100	50	Dirt and Leaf Litter
Shamba	2.5	0	75	Dirt and Grass
Shamba	3.5	90	100	Leaf Litter

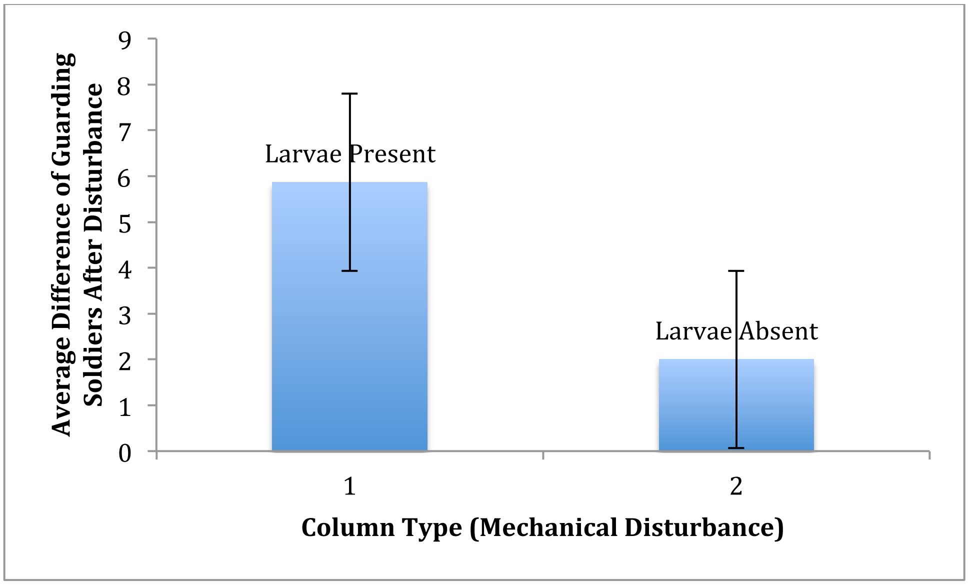

Figure 2. Mean difference (+SE) of guarding soldiers before and after mechanical disturbance in LP and LA columns near the Mazumbai Forest Reserve (n=30).

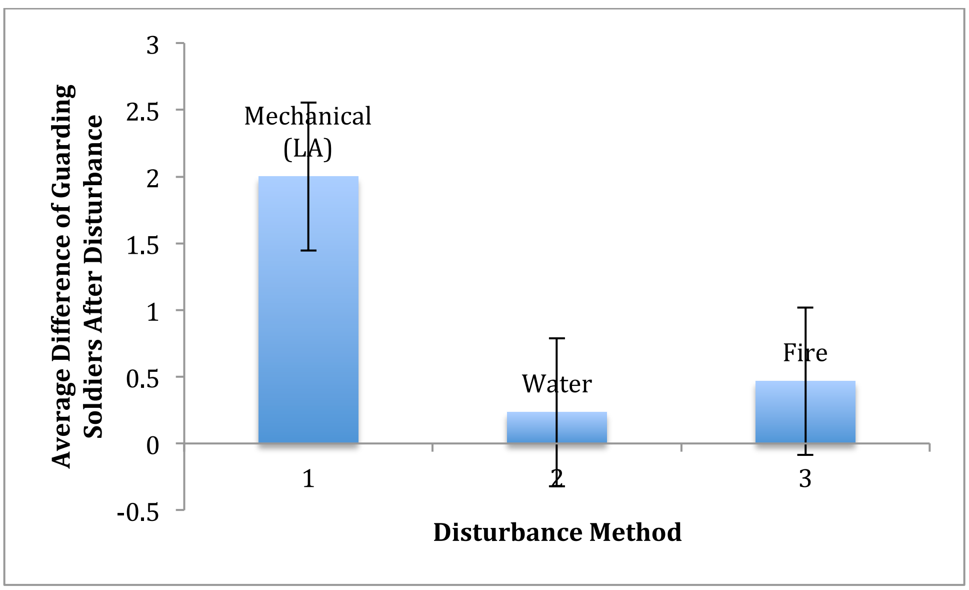

Figure 3. Mean difference (+SE) of guarding soldiers before and after mechanical, water, and fire disturbances in LA columns within and around the Mazumbai Forest Reserve (n=30).

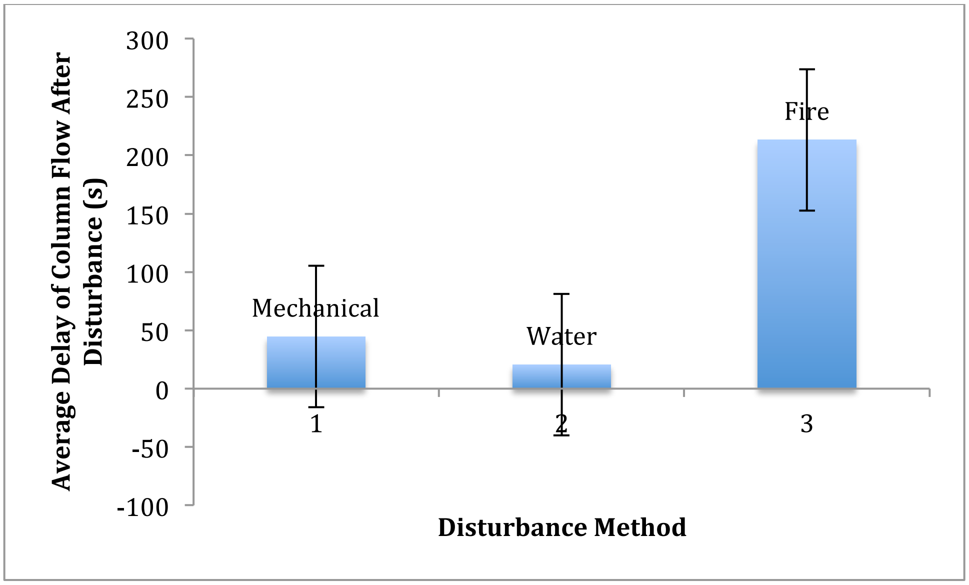

Figure 4. Mean time (+SE) until the return of normal column flow following mechanical, water, and fire disturbance within and around the Mazumbai Forest Reserve (n=30).

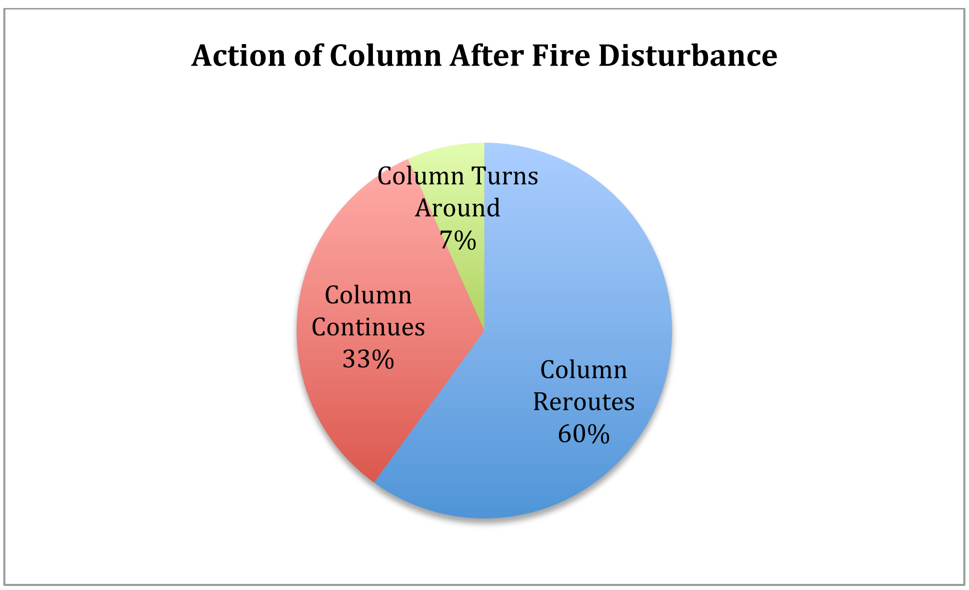

Figure 5. Behavior of LA columns in response to fire disturbance around the Mazumbai Forest Reserve (n=30).

DISCUSSION

The response of Siafu soldiers to varied disturbance methods was measured on columns with larvae present and larvae absent. Siafu were found to respond differently to each of the disturbance types. LP and LA columns were also found to respond differently to mechanical perturbations. The amount of time it took for columns to return to normal flow, as well as their reactions, were dependent on the type of disturbance. Novel nest and column characteristics were also found and described. As mentioned in the introduction, almost no data is available for Tanzanian Driver Ants. Some observations could be new and unclassified at this time.

The scaffolding behavior of ants within columns appeared to be a protective tactic as well as a defensive one. While it is most apparent that these areas of scaffolding are meant to provide increased protection in places where the column is most exposed to the environment, the masses of interlinked ants might also create shade for the smaller workers moving underneath. This is an important task considering that the ants are strongly deterred by sunlight (Garey 2015). The study by Garey observed ants that were exhibiting seizing behavior in open areas such as roads, where sunlight and heat were the most intense. This behavior is most likely caused by overheating. The small body size of the ants, and their surface area to volume ratio, makes them more susceptible to radiation. Ants were found to die very quickly when close to fire, or even when dropped in warm water. Protecting the larvae and workers from the intense Tanzanian sunlight is important for the survival of the colony. The scaffolding masses were also thick enough to repel water in some places.

The Velcro-like massing of the ants is a characteristic common to other species of army ant. Hypogeic species, such as *Dorylus laevigatus,* create large masses of linked ants above the ground, a structure known as a bivouac (Berghoff et al. 2002). It is possible that the wall of ants described within the nest found in the forest was one of these structures. These large, motionless masses of ants are usually complete with tunnels and compartments much like a normal ant colony underground (Berghoff et al. 2002). Bivouacs in other driver ant subspecies are known to be hypogeic however, and not epigaiec like the Siafu.

While it was previously though that there were only 4 different morphs of Siafu workers, I argue that there are at least 6 (Fig.1). Driver ants are holometabolous, meaning they have 4 stages in their life cycles: egg, larva, pupa, and adult. When adults emerge from the pupal stage, they are fully-grown, and do not expand in size throughout their lifetime (Schabel 2006). Therefore, any difference in ant size must signify a unique morph of ant. While it is possible for insects such as ants to differ slightly in their size, it is unlikely that ants in the same morph would differ by more than a millimeter.

While Garey (2015) describes soldiers as having the primary duty of guarding the columns, I found that workers were present much more often than soldiers in guarding behavior. Soldiers in columns and in raids were used for guarding, sectioning up and carrying large pieces of prey, and clearing large debris from out of the path. This behavior is common to polymorphic ants, where prey sizes are often correlated with prey retrieval ability (Gotwald 1974). Soldiers had a much higher presence and density inside the nest, where their increased power and ability to deter predators is more appropriately used in order to protect the queen and the young (Oster & Wilson 1978). Specialized predators, such as the Pangolin (*Manis temincki*), are one of the few successful predators of Siafu. The ability to fend off these mammals and other predators from the nest is paramount.

The behavior of the ants in response to other insects is often more docile than expected. The silverfish-like insect that was observed in the nest may have been a mutualist towards the ants, as some species of beetles are known to do. Rove beetles, in particular, are known to live inside Siafu nests, and can sometimes be used as predictors of a nest move because of their exodus from a nest site (Schabel 2006). The orange beetles, described by Garey (2015) are most likely a species of the same vain, living in a mutualistic relationship with the ants. However, it is possible that the ants were not in a position to attack them.

Ants release a variety of communicative pheromones, which they use for foraging, identifying threats, and recognition of colony members (Jackson &

Ratnieks 2006). When ants are foraging, they release different pheromones compared to when they are not. I briefly experimented with this behavior by offering different column types pieces of food. The egg columns completely ignored the food item, a large black bee that I had found nearby, and attempted to move the bee out of their path before completely ignoring it. But when the bee was moved to a raiding column, the ants swarmed it and sectioned it up. It is likely that this behavior was indicative of the different hormones present in different situations. Ants carrying larvae must exude hormones that negate the instincts of capturing food, as it would leave the precious larvae exposed. However, raids, which would have those specific pheromones to incite foraging behavior, are ravenous in their pursuits. The ability to communicate between individuals is an evolutionary advantage, which allows the ants to forage more efficiently. Areas where raids were underway could easily be identified by the complete absence of all other observable insect life.

Pheromones are most likely responsible for the reactions of the ants to disturbances. Repeat disturbances were common on roads and footpaths where motorcycles and human traffic constantly ran over columns. Dead ants release pheromones that cause other ants to go into a state of frenzy, creating panic and aggressive behavior (Jackson & Ratnieks 2006). These sections were often so thick with ants that they could be seen long before arriving at the column. While repeated disturbance was not the main focus of this study, the behavior of the ants to reinforce sections of the column with the most disturbance is key to understanding their responses to different types of disturbance as described later in this study.

As described by Garey (2015), ant columns will actively move out of sunlight if shaded routes are accessible. In the forest, columns moved exclusively under leaf cover, making them difficult to find. The ants moved over exposed ground only when they had to, usually on roads or manicured grass. Nests displayed similar characteristics as the columns in that they were most often found under some sort of shade or cover (Table 1). Nests were also always found on steep slopes of banks or under tree roots. This is most likely due to the ease of excavation and increased protection from the elements. The Siafu are not as adept at burrowing as other species in the area (Garey 2015). Having easily accessible routes into the ground is helpful for the nomadic ants to quickly build nests and protect their queen and young. Also, building the nests on a slope could also help with water drainage. The rainy season in Tanzania brings a large volume of water into Siafu columns and nests. Within proper protection from the rains, colonies would most likely drown and perish.

The movement of nest sites is known to occur every couple of days for most army ant species (Oster & Wilson 1978). In this study, a nest was observed moving into an area, and then moving out of it. The proximity of the nest to a large pile of rotting garbage was probably not a coincidence: nests most likely move towards areas of high food density, and abandon those sites when food becomes scarce. However, the colony came in from the north, and continued south when it moved on. It is also possible that the ants follow magnetic fields from the earth, as other species are hypothesized to do (Jackson & Ratnieks 2006). However, this concept is not well studied.

The mechanical disturbance of LP and PA columns, more soldiers were observed in a guarding posture in the LP columns after perturbation (Fig. 2). Due to the importance of the larvae to the future of the colony, the need for protection in columns transporting them is greater than those that are foraging for food or scouting for it. Garey (2015) observed this trend in LP columns as well, noting that they also tended to be the densest. Although the density of these columns must have an effect on the number of soldiers present, the average difference of soldier abundance was still greater in LP columns than in LA columns, a figure that should be independent of density.

The mechanical disturbance probably displayed the highest increase of soldiers due to evolutionary responses to predators such as the Pangolin described previously (Fig. 3). Mechanical disturbance, such as the one performed in this study, represent an aggressive agitation caused by fauna. The response of the soldiers to this type of disturbance would have to be aggressive in order to combat the imagined attack and protect the colony. This phenomenon probably explains why it took more time for column flow to return to normal in the mechanical disturbances compared to the water disturbances (Fig. 4). The water disturbance was expected to cause the least observable difference in soldier presence, which it did. This was hypothesized due to the high degree of rainfall and water disturbance already present in the region. If ants spent significant amounts of energy and manpower defending the colony from sections affected by rainfall, mistaking it for an aggressor, they would inevitably leave other sections of the column or nest less protected. At the same time, if the ants spent excess time stationary after a water disturbance rather than moving through it quickly, they would not be able to forage as efficiently or timely, or would take longer to transport their larvae in exposed environments. In this way, the ants display dynamic distribution of resources in their defense.

The fire disturbance, however, was predicted to cause the greatest increase of soldiers due to the degree of the disturbance and the death of ants caused by it. This was not shown in the data. Instead, soldier presence remained relatively constant, most likely due to the fires effect on the chemoreception of the ants. As described previously, pheromones and the chemical reception of them by the ants' antennae is key to ant communication (Jackson & Ratnieks 2006). The ability of the ants to continue along their column paths is inevitable decided by these chemicals. If the chemical trail is disrupted, the ants are left blind to their surroundings. The fire disturbances most likely disrupted this chemical signaling pathway by denaturing or removing the chemical trails laid down by the ants. While the mechanical and water disturbance tests slowed the column flow to some degree, all of the columns in these trails continued eventually along the same path. However, a majority of the fire-tested columns rerouted around the area of the burn, or turned around completely, abandoning the path altogether (Fig. 5). With the chemical trails destroyed, the ants would have to create a new path around or through the burn area, which they often did. Also, as the ants were delayed, they tended to ball up before and after the area of disturbance. This leaves them more vulnerable, as they are easier to spot for predators, more subject to death by solar radiation, and at greater risk of being run over or stepped on.

Projecting the implications of this study into the future, considering the looming environmental changes coming to the area, is difficult to do. While the ants appear to be somewhat resistant to disturbance, larger, and repeated perturbations could have a more pronounced effect on the wellbeing of Siafu colonies. Increasing numbers and sizes of brush fires could greatly inhibit the Siafu's ability to find food and maintain column flow. Inhibiting the flow of columns will most likely create more situations where the ants are vulnerable. However, in terms of the fragmentation of the forests, it appears that the Siafu will not be severely threatened. A study by Schoning et al. (2006) found that Siafu presence was not correlated with forest patch size or the distance between patches. Indeed, many of the columns and nests observed in this study were found in edge habitats and non-forested farmland. While it is hard to say that the ants will persist in the face of deforestation, increased human activity will definitely affect the functioning of the Siafu in the near future.

For this purpose, further studies on the ants in this region should be explored. I believe that these ants are very important not only to the ecosystem and the balance of prey species, but also for agriculture and pest control in farms. The Siafu perform an important role in pest control, possibly representing a better alternative to pesticides. The degree of insect removal that these ants are responsible for is vastly understudied, and should be focused on in the future. It would also be important to explicitly test and map out how the distribution of columns and nests relates to fragmentation in the Usumbara Forests. Also, these ants could be used as an alternative protein source. With an increasing population and an already existing protein deficiency in Tanzanian populations, eating these ants, which are relatively easy to find and capture in large numbers, offers an opportunity to satiate that deficiency. With proper extraction and harvesting practices, the ants could be used as a renewable food source.

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APPENDIX A:

Location of the West Usumbaras in northern Tanzania. The marker indicates the location of Mazumbai Forest Reserve. Image taken from Google Maps.

APPENDIX B:

All photos and videos that were taken for this study can be found online by messaging me on Facebook or emailing me at beckenbauerrm@gmail.com. Facebook will be more reliable.